FLOWERS AND INSECTS. XX

EVOLUTION OF ENTOMOPHILOUS FLOWERS

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In his *Fertilisation of flowers* (pp. 594, 595) MÜLLER arrives at the following conclusions with regard to the development of flowers:

The transition from wind fertilization to insect fertilization, and the first traces of adaptation to insects, could only be due to the influence of quite short-lipped insects with feebly developed color-sense. The most primitive flowers are therefore for the most part (except, for instance, *Salix*) simple, widely open, regular, devoid of honey or with their honey unconcealed and easily accessible, and white or yellow in color (for example, most Umbelliferae and Alsineae, many Ranunculaceae and Rosaceae).

Gradually, from the miscellaneous lot of flower-visiting insects, all much alike in their tastes, there arose others more skilful and intelligent, with longer tongues and acuter color-sense; and they gradually caused the production of flowers with more varied colors, honey invisible to or beyond the reach of the less intelligent short-tongued guests, and various contrivances for lodging, protecting, and pointing out the honey.

The Ichneumonidae at first surpassed all other visitors in observation and discernment, and they were thus able to produce inconspicuous flowers which escaped the notice of other visitors. On the appearance of sand wasps and bees these inconspicuous flowers were banished by competition to the less frequented localities (for example, *Listera* to shady woods).

The sand wasps (Sphegidae) apparently took the place to a great extent of the ichneumons, and produced flowers where organs had to be thrust apart (Papilionaceae), or where a narrow cavity had to be entered (Labiatae), or where some other action similar to the act of digging had to be performed. Subsequently bees seem to have entered on joint possession of most of these flowers, and to have added special adaptations of their own.

The true wasps (Vespidae) could establish themselves by the fear of their sting (and of their jaws) in sole possession of certain flowers with wide open mouths and abundant honey. These they developed further in relation to their wants (*Scrophularia, Symphoricarpos, Epipactis latifolia, Lonicera alpigena*); but where wasps are scarce the flowers are utilized by other insects.

Bees (Apidae), as the most skilful and diligent visitors, have played the chief part in the evolution of flowers; we owe to them the most numerous, most varied, and most specialized forms.

Whether the primitive flowers were pollinated by wind or by insects is uncertain. The forms of flowers which preceded the angiosperms were probably entomophilous. The carpels closed over the ovules to form an ovary and the stigma was developed to receive the pollen. The stigma and closed ovary are regarded as entomophilous characters and as having been developed after the visits of insects were established. The origin and development of entomophilous flowers, no doubt, were connected with the origin and specialization of the bees, Hymenoptera which adopted the habit of provisioning their nests with nectar and pollen. Along with the acquisition of this habit, the bees developed a coat of feathery hairs to which the pollen might cling, these hairs on certain parts of their bodies, as the hind legs and the ventral surface of the abdomen, being greatly modified to form a special pollen-carrying apparatus. Thus the pollen became absolutely essential in the economy of the bees. To the flowers, on the other hand, the bees became important visitors, because they had to resort to flowers frequently and because they were provided with a coat specially fitted to retain the pollen, and at the same time exerted themselves to get the coat as full of pollen as possible.

Bees, as we know them, visit flowers both for nectar and for pollen, but it is possible that the primitive bees visited flowers only for pollen and that the secretion of nectar came after.

The view has been expressed[1] that the ordinary short-tongued bees can collect only viscid pollen, and that therefore they could have begun to use pollen to provision their nests only after pollen had become sticky in adaptation to insect pollination. Species of *Chloralictus* collect the dry pollen of grasses and of *Plantago*, however, and ordinary bees collect from a considerable number of flowers pollen which is so dry that it pours out as soon as it is released from the anthers. So bees may have commenced to collect pollen when only dry pollen existed. The fact that bees are the most highly specialized of Hymenoptera, and the latest developed, does not prove, and does not seem to establish a reasonable presumption, that any considerable evolution of entomophilous flowers preceded their advent.

[1] ROBERTSON, CHARLES, Flowers and insects. XIX. BOT. GAZ. **28**:39. 1899.

Putting speculation aside, the further consideration of this subject will be limited to the structure and affinities of the flowers, and the behavior of the insects which we know. Social flowers are those which are so closely approximated that the visitors may readily pass from one to another without taking wing or climbing. They are usually found in heads, spikes, or close umbels. The simplest flowers which we know are non-social flowers of class *AB*, flowers with partly concealed nectar. Insect visits to them show:

	Species	Bees	Diptera	Other Hymenoptera	Lepidoptera	Coleoptera Hemiptera	Total
Class *AB*.....	41	56.8	31.2	4.7	4.8	2.3	866
Visits.....	14	43.7	32.8	19.5	2.7	1.2	405
Individuals.....	0	70.2	20.4	8.0	0.7	0.5	2438

These are evidently bee flowers, although they are not exclusively visited by bees. No insects except bees prefer flowers of this kind. There are no non-social flowers of class *AB* which are adapted to miscellaneous insects or to particular kinds of visitors except bees. On 14 species of class *AB* bees showed 43.7 per cent of the visits and 70.2 per cent of the individuals. Of course it is possible that the primitive non-social flowers of class *AB* were visited by a miscellaneous set of the least specialized anthophilous insects. If so, the short-tongued bees must have tended early to monopolize them, while the other insects paid more attention to the forms which became social.

Observations of 221 visits to 17 non-social flowers of class *A*, flowers with exposed nectar, show: bees 33.4, Diptera 45.7, other Hymenoptera 14.4, Coleoptera and Hemiptera 6.3. Here the Diptera predominate, and the group is rather miscellaneous. Some of the group are distinct fly-flowers (*Asimina triloba*); some are quite simple (*Asimina*, *Myosurus*, and *Caulophyllum*). The dark color and pendulous position of *Asimina* are hardly typical, and *Myosurus* and *Caulophyllum* have peculiar petals. None of these are simple like ordinary non-social flowers of class *AB*. Most non-social *A* have epigynous nectaries (*Hypoxis*, *Circaea*,

Galium). A characteristic flower is *Circaea lutetiana*. Its visitors are:

	Bees	Diptera	Total
Species	81.8	18.1	11
Individuals	94.0	5.9	84

Class *A* is a poor place to look for simple flowers. The majority are social and have epigynous nectaries, both forms of specialization. Except class *B*,[1] this class is the only one in which the majority of the species are social. The visits to 23 social *A* are as follows: bees 21.9, Diptera 38.3, other Hymenoptera 27.3, Lepidoptera 2.6, Coleoptera and Hemiptera 9.6, making a total of 2335.

Table I, based on 10,041 visits, shows the percentages of visits of all classes to flowers adapted to short-tongued insects, usually small flowers with nectar exposed, partly or wholly concealed, but never deep seated.

TABLE I

	Bees	Diptera	Lepidoptera	Coleoptera	Hemiptera	Lower Hymenoptera
			PERCENTAGE OF VISITS			
To non-social flowers	18.1	12.4	11.2	8.6	6.1	4.1
To social flowers	41.8	73.5	34.8	83.3	78.7	84.9
			PERCENTAGE OF TOTAL VISITS			
To non-social flowers	59.5	25.3	7.2	2.0	0.3	5.3
To social flowers	31.0	33.8	5.0	4.4	1.0	24.4

Of the visits of bees, 18.1 per cent are to non-social small flowers, and these form 59.5 per cent of the total insect visits to such flowers. Sixteen non-social small flowers, on which the individual insects were taken as they came and counted, showed 335 visits and 1520 individuals. The percentage of bee visits was 59.1, but of bee individuals 74.2, showing that bees are more important than the percentage of visits indicates.

The relations of bees and other insects to non-social and social flowers in general (based upon 13,942 visits of 1287 insects to 437 flowers) are shown in table II.

TABLE II

	Lower Hymenoptera	Hemiptera	Coleoptera	Diptera	Lepidoptera	Bees	All Except Bees	Total
PERCENTAGE OF VISITS								
To non-social flowers.....	4.4	6.1	9.3	13.6	22.6	32.1	11.9	20.7
To social flowers.....	95.5	93.8	90.6	86.3	77.3	67.8	88.0	79.2
PERCENTAGE OF TOTAL VISITS								
To non-social flowers.....	3.6	0.2	1.4	17.8	9.3	67.4	32.5	99.9
To social flowers.....	20.4	0.9	3.5	29.4	8.3	37.2	62.7	99.9

Of the total visits of bees, 32.1 per cent are to non-social flowers, and these form 67.4 per cent of the total insect visits to such flowers. Of the total visits of other insects to non-social flowers, the percentage is 4.4 for lower Hymenoptera, 6.1 for Hemiptera, 9.3 for Coleoptera, 13.6 for Diptera, and 22.6 for Lepidoptera; or a general percentage of 11.9. Since bees make over two-thirds of the insect visits to non-social flowers, it is evident that they have been chiefly instrumental in the origination of such flowers.

Of the total visits of bees, 67.8 per cent are to social flowers, so that bees show a strong preference for these flowers also, although not as strong a preference as the Lepidoptera with 77.3, the Diptera with 86.3, the Coleoptera with 90.6, the Hemiptera with 93.8, and the lower Hymenoptera with 95.5 per cent.

One might suppose, with MÜLLER, that the non-aculeate Hymenoptera have had an influence in the development of some primitive flowers, and that these flowers were further modified by the aculeate Hymenoptera, and finally became highly specialized in connection with the development and specialization of the bees. When, however, we look for such flowers, we find only the so-called ichneumon flowers, *Listera ovata* and *Chamaerorchis alpina*, belonging to the most highly specialized of monocotyledons. In the

case of the Ichneumonidae only 2.5 per cent of the visits are to non-social flowers.

The only flowers supposed to have been modified by the Vespidae are the so-called wasp flowers, *Epipactis latifolia* (Orchidaceae) belonging to the most highly specialized group of non-social monocotyledons, *Scrophularia nodosa* (Scrophulariaceae) belonging to a distinctly melittophilous family, *Lonicera alpigena* belonging to a melittophilous genus, and *Symphoricarpos racemosus* belonging to the epigynous Caprifoliaceae. None of these belong to primitive forms of flowers which might have preceded the advent of the bees. Only 8.7 per cent of the visits of Vespidae are to non-social flowers.

With the exception of *Symphoricarpos*, all of the flowers mentioned by MÜLLER as having been modified in adaptation to the lower Hymenoptera are zygomorphous: Orchidaceae, Papilionaceae, Labiatae, *Scrophularia*, and *Lonicera alpigena*. Zygomorphous flowers, except such forms as *Aristolochia*, with *siphonate* zygomorphy, and the outer flowers of the umbels of *Heracleum*, with *radiate* zygomorphy, are typically non-social and adapted to bees which visit each flower separately. They have a landing either above or below the stamens and pistils and usually dust the visitor on the lower or upper side. It is fairly inconceivable that zygomorphy should have originated in crowded inflorescences where the flowers might be approached from any side. Excluding such flowers as *Heracleum*, *Aristolochia; Amorpha*, *Petalostemon*, and *Melilotus* in Papilionaceae; and *Pycnanthemum*, *Lycopus*, and *Mentha* in Labiatae, 100 zygomorphous flowers show: bees 74.3, Diptera 8.5, other Hymenoptera 9.1, Lepidoptera 7.1, Coleoptera and Hemiptera 0.7, making a total of 1117 visits.

Visits to the Papilionaceae show:

	Bees	Diptera	Other Hymenoptera	Lepidoptera	Coleoptera, Hemiptera	Total
Non-social (24)	97.5	1.6	0.8	0.0	0.0	123
Social (9)	56.1	16.3	23.0	1.5	2.9	447
Total (33)	65.0	13.1	18.2	1.2	2.2	570
Amorpha, etc. (4)	45.3	18.5	29.4	2.3	4.3	302

When the lower Hymenoptera together make only 0.8 per cent of the visits to the non-social Papilionaceae, it is evident that they have had little to do with the evolution of the Papilionaceae, even if they were instrumental in their origin. To support the latter condition it would be necessary to show that the non-social forms were developed from the social forms.

Visits to Labiatae show:

	Bees	Diptera	Other Hymenoptera	Lepidoptera	Coleoptera, Hemiptera	Total
Non-social (13)	83.1	5.8	0.8	10.0	0.0	119
Social (12)	39.5	20.8	24.6	12.7	2.2	897
Total (25)	44.6	19.0	21.8	12.4	1.9	1016
Lycopus, etc. (5)	29.6	24.6	34.5	7.8	3.2	576

When the lower Hymenoptera show 24.6 per cent of the visits to social Labiatae and only 0.8 per cent to non-social Labiatae, it is hard to connect them with the origin of the Labiatae unless we suppose that the non-social developed from the social. MÜLLER (*Fertilisation of flowers*, p. 471) says: "DELPINO considers *Mentha* and *Coleus* degraded forms of the labiate type; he, however, gives no reason for thinking them to be such, and not rather less specialized forms, differing less from the common ancestors of the Labiatae." If there are non-social zygomorphous wasp flowers or ichneumon flowers, no doubt they should be regarded as modified from bee flowers.

The view held here, that the early flowers were non-social and were modified in connection with the visits of bees, and that the flowers mainly visited by other insects are later, is supported by what is known of the behavior of insects and by inferences from the affinities of the flowers. Of course, if it can be shown that the primitive flowers were social and that the non-social flowers were developed from them, this view will have to be abandoned for that of MÜLLER.

Of the total visits of the lower insects, 88.0 per cent are to social flowers, and of the total insect visits to social flowers the lower insects make 62.7 per cent. Now the flowers which these insects

prefer are not the simple ones, but the majority are social and have epigynous nectaries.

The original or normal bees are polylectic. They have a general relation to the flora and more special relations to certain flower classes. From these have originated the oligolectic bees and inquilines. The oligoleges collect pollen exclusively from flowers belonging to particular natural groups. They do not prefer flower classes except in so far as their particular flowers happen to belong to those classes. The inquiline bees live in the nests and at the expense of the other bees. They get only nectar from the flowers which happen to be the most convenient and easiest for them to visit. The importance to the flora of these 3 sets of bees is partly indicated in table III.

TABLE III

	Species	Visits	Average
Normal, polyleges	132	4448	33.6
Inquilines	72	781	10.8
Oligoleges	83	668	8.0
Prosopis	9	166	18.4
Total	296	6063	20.4

In a considerable number of polyleges the flight of the males is quite different from that of the females. The males do not make half as many visits as the females, and the flowers which they visit are so different that their visits to flowers should be considered separately. Table IV shows the differences.

TABLE IV

	Females (♀ excluded)			Males		
	Number	Visits	Average	Number	Visits	Average
Large polyleges	50	1239	24.6	50	806	16.1
Small polyleges	72	2098	29.1	64	722	11.2
Total	122	3337	27.3	114	1528	13.3

The groups of visitors preferring certain classes of non-social flowers are separated as shown in table V. Usually large flowers

with deep seated nectar are referred to as *Ma*, usually small flowers with nectar not deep seated are referred to as *Mi*, while *Pol* indicates the extreme social forms.

TABLE V

	Non-social			Social				Total
	Ma	Mi	Total	Ma	Mi	Pol	Total	
Flora	30.2	24.2	54.4	18.7	21.5	5.2	45.5	437
Small bees, polyleges ♀	5.0	30.4	35.5	11.7	43.6	9.0	64.4	2098
Large bees, polyleges ♀	35.9	13.4	49.4	30.9	15.8	3.7	50.5	1239
Sphingidae	54.5	0.0	54.5	40.9	4.5	0.0	45.4	22
Humming-bird (*Trochilus*)	82.7	3.4	62.2	13.7	0.0	0.0	13.7	29

The females of the short-tongued polylectic bees form the only group of insects preferring non-social *Mi*. They are credited with the origin of such flowers. The females of the long-tongued polylectic bees, the Sphingidae, and *Trochilus* are the only groups preferring non-social *Ma*. This is the largest flower class, originally modified by long-tongued bees. The Sphingidae and *Trochilus* prefer such flowers and in some cases have entirely appropriated them.

As flowers have become social they have been preferred in the order shown in table VI.

TABLE VI

Groups of insects	Non-social	Social
Large bees, polyleges ♂	37.8	62.1
Lepidoptera (ex. Sphingidae)	22.0	77.9
Large bees, inquilines	20.6	79.3
Small bees, polyleges ♂	19.5	80.4
Prosopis	13.8	86.1
Diptera	13.6	86.3
Large bees, oligoleges	13.4	86.5
Small bees, inquilines ♀	12.7	87.2
Small bees, oligoleges	11.3	88.6
Coleoptera	9.3	90.6
Hemiptera	6.1	93.8
Lower Hymenoptera	4.4	95.5
Small bees, inquilines ♂	4.0	96.0

Some female bees on their pollen visits show a preference for social flowers. Eighty-five species of long-tongued bees, with

806 pollen visits, and 1155 nectar visits of females and workers, show the following percentages of visits to social flowers with exposed pollen: for nectar 41.1; for pollen 49.2. Compared with the visits of the females for nectar, the females when collecting pollen make 8.1 per cent more visits to social flowers.

There are some large social inflorescences composed of flowers with exposed or only slightly concealed nectar. Long-tongued bees practically avoid them on their nectar visits, but often visit them for pollen. Such are *Cornus*, *Hydrangea*, and *Viburnum*. *Vitis*, with exposed nectar, seems to be an important source of pollen for female bumblebees. The aggregation of flowers in social clusters has been interpreted as an adaptation for gitonogamy, but it occurs about as often in cases where gitonogamy is impossible.

Finally, the evolution of entomophilous flowers is held to have proceeded in the following manner. The primitive flowers were non-social flowers of class *AB*, with partly concealed nectar, adapted to short-tongued bees. These have produced flowers with exposed nectar more favorable to flies, and flowers with more concealed nectar still more favorable to bees. A few have become adapted to flesh flies (*Asimina*), and others to minute flies (*Aristolochia*).

The non-social small bee flowers have produced social forms still favoring small bees, but admitting other short-tongued insects. These finally pass into the extreme social forms which have become modified to suit miscellaneous short-tongued insects.

The non-social small bee flowers have been modified further and developed into non-social long-tongued bee flowers. Some of these have been appropriated by birds and others by Sphingidae, and perhaps still others by butterflies.

The non-social long-tongued bee flowers have also been modified into social forms attracting Lepidoptera and long-tongued Diptera. These are still considered as bee flowers, but some of them may more properly be regarded as adapted to miscellaneous long-tongued insects. The social long-tongued bee flowers also pass into social short-tongued bee flowers, and finally into social flowers adapted to miscellaneous short-tongued insects.

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